

Relevant Elements, Magnetization and Dynamical Properties in Kauffman Networks: a Numerical Study.

U. Bastolla^{1, 2} and G. Parisi¹

February 1, 2008

¹Dipartimento di Fisica, Università “La Sapienza”, P.le Aldo Moro 2, I-00185 Roma Italy

²HLRZ, Forschungszentrum Jülich, D-52425 Jülich Germany

Keywords: Disordered Systems, Genetic Regulatory Networks,
Random Boolean Networks, Cellular Automata

Abstract

This is the first of two papers about the structure of Kauffman networks. In this paper we define the relevant elements of random networks of automata, following previous work by Flyvbjerg [5] and Flyvbjerg and Kjaer [6], and we study numerically their probability distribution in the chaotic phase and on the critical line of the model. A simple approximate argument predicts that their number scales as \sqrt{N} on the critical line, while it is linear with N in the chaotic phase and independent on system size in the frozen phase. This argument is confirmed by numerical results. The study of the relevant elements gives useful information about the properties of the attractors in critical networks, where the pictures coming from either approximate computation methods or from simulations are not very clear.

1 Introduction

Kauffman networks are disordered dynamical systems proposed by Kauffman in 1969 as a model for genetic regulatory systems [1]. They attracted the interest of physicists in the 80's [2, 3, 4, 5, 6], due to their analogy with the disordered systems studied in statistical mechanics, such as the mean field Spin Glass [7]. A dynamical phase transition was found and studied in the framework of mean field theory.

In this and in the next paper [8] we deal with some structural properties of the networks that determine their attractors. In the present paper we introduce the relevant elements, a notion that was suggested by Flyvbjerg [5] and Flyvbjerg and Kjaer [6], and we study their probability distribution. In the next one we describe how the relevant elements are subdivided into asymptotically non communicating, independent modules. The modular organization of random boolean networks was already suggested by Kauffman [1], and it was used by Flyvbjerg and Kjaer to study analytically the attractors in $K = 1$ networks. We shall show that it is possible to describe the phase transition in random boolean networks

in terms of the scaling of the number of relevant elements with system size, or in terms of a percolation transition in the set of the relevant elements. The interest of this approach is that some consequences about the statistical properties of the attractors can be directly drawn.

In [9] we computed the properties of the attractors in the framework of the annealed approximation, introduced by Derrida and Pomeau [2], but we observed that the results of this approximation are reliable only when the system is chaotic enough, becoming exact for a random map. The study of the relevant elements is complementary to this approach, and we sketch the lines of a new approximation scheme that works better in the frozen phase and on the critical line. This region in parameter space is the most interesting one, since, according to Kauffman, it reproduces some features of real cells, and is also the less understood, since neither approximate computations nor simulations [10] give a precise picture of the properties of the attractors for systems of large size.

In next section we define the model, discussing some old results together with open problems. In section 3 we define the relevant elements and in section 4 we give an approximate argument predicting the scaling of their number with system size in the different phases of the model. In the following section we present our numerical results, starting from the magnetization and the stable elements (section 5.1) and then discussing the distribution of the relevant elements and its connection with the properties of the attractors, respectively in the chaotic phase (section 5.2) and on the critical line (section 5.3). The discussion of the results is postponed to our following paper [8], concerning the modular organization of the relevant elements on the critical line.

2 Definition of the model and previous works

Kauffman model is defined as follows. We consider a set of N elements $\Omega = \{1, \dots, N\}$ and we associate to each of them a binary variable, $\sigma_i \in \{0, 1\}, i \in \Omega$. In the biological interpretation proposed by Kauffman each element of the network represents one gene and the binary variable σ_i represents its state of activation.

Each element is under the control of K elements, in the sense that its state at time $t + 1$ is determined by the states at time t of the K control genes, $j_1(i), \dots, j_K(i)$ and by a response function of K binary variables, $f_i(\sigma_1, \dots, \sigma_K) \in \{0, 1\}$, that specifies how the element i responds to the signals coming from its control variables. The control elements are chosen in Ω with uniform probability. The response functions are also extracted at random, and it's believed that the properties of the model do not depend on the details of their distribution [5, 9, 10]. The rule most generally used in the literature is the following: for each of the possible inputs $\in \{0, 1\}^K$ we extract independently the value of f_i , and we call p the probability that f_i is equal to 0.

The dynamics of the system obey the equation

$$\sigma_i(t + 1) = f_i(\sigma_{j_1(i)}, \dots, \sigma_{j_K(i)}). \quad (1)$$

This evolution law is deterministic, but the system is disordered because the control rules (elements and functions) are chosen at random from the beginning and kept fixed: thus we deal with a statistical ensemble of deterministic dynamical systems, and we are interested

in the statistical properties of systems of large size. For finite N , every trajectory becomes periodic after a long enough transient time, and the configuration space is partitioned into the attraction basins of the different periodic orbits. We are interested in the probability distributions of the number, the length and the size of the attraction basin of the periodic orbits, as well as in that of transient times. In the biological metaphor, given a set of rules (a genome) an attractor represents a possible cellular type, its length represents the duration of the cellular cycle, and the number of attractors represents the number of cells that can be formed with a given genome.

It was observed already in the first simulations that two dynamical regimes are present, and that the line separating them has properties reminiscent of those of real cells [1]. In the so-called chaotic phase (large connectivity, p close to $1/2$) the average length of the cycles increases exponentially with system size. The limit case of the chaotic phase, $K \rightarrow \infty$, was already known as Random Map in the mathematical literature, and was studied in detail by Derrida and Flyvbjerg [11], who pointed out interesting analogies between this system and the mean field Spin Glass [7] concerning the distribution of the weights of the attraction basins. In the frozen phase, on the other hand, the typical length of the cycles does not increase with N . The limit case of this phase, $K = 1$, was analytically studied to some extent by Flyvbjerg and Kjaer [6], who introduced in that context the concept of relevant elements (though without using this name).

The first description of this dynamical phase transition in terms of an order parameter was given by Derrida and Pomeau [2]. They studied the evolution of the Hamming distance between configurations in the Kauffman networks approximating it with a Markovian stochastic process. Such approximation (the so-called annealed approximation) was then shown to be exact in the infinite size limit, concerning the average value of the distance [3]. Below a critical line in parameter space the average distance goes to zero in the infinite size limit (*frozen phase*) and above it the distance goes to a finite value (*chaotic phase*). The position of the phase transition depends only on the parameter ρ , representing the probability that the responses to two different signals are different¹, and is given by the equation $\rho_c(K) = 1/K$.

The properties of the attractors can be easily computed from the knowledge of the whole stationary distribution of the distance, and this can also be obtained within the annealed approximation [9], but the validity of this approximation in this more general case is not guaranteed. Comparison with simulations shows that the agreement is satisfactory in the chaotic phase, while the approximation fails on the critical line. In the chaotic phase it is possible to compute the value of the exponent of the typical length of a cycle, $\tau \propto \exp(\alpha(K, \rho)N)$, in good agreement with numerical results, but the distribution of cycle lengths is much broader than it is expected. The annealed approximation predicts also that the distribution of the weights of the attraction basins is universal in the whole chaotic phase, and equal to the one obtained by Derrida and Flyvbjerg in the case of the Random Map [11]. The corrections to this prediction appear small, if any, even for $K = 3$. Finally, the number of different cycles in a network is expected to be linear in N , but it is very hard to test numerically this prediction.

The annealed approximation makes also predictions about the critical line of the model

¹In terms of p one has $\rho = 2p(1 - p)$, so its value is comprised between zero and $1/2$, but for $K = 1$ ρ can be taken as an independent parameter in $[0,1]$

[9]. It predicts that the properties of the attractors are universal on the critical line $\rho = 1/K$ (with the exceptions of the points $K = 1, \rho = 1$ and $K = \infty, \rho = 0$, which are not transition points). In particular, the typical length of the cycles should increase as \sqrt{N} all along the critical line. Numerical results are not clear under this respect [10]: it seems that the rescaled cycle length $l = L/\sqrt{N}$ has a limit distribution if l is small (roughly, smaller than 2) but for larger values the distribution becomes broader and broader as N increases [12, 10], so that it is possible to define an effective length scale increasing much faster with system size (as a stretched exponential). The distribution of the number of cycles has exactly the same characteristics. These results cast doubts on the validity of the biological analogy proposed by Kauffman, that relies very much on the fact that in critical networks the typical number of cycles scales as \sqrt{N} , reminiscent of the fact that the number of cell types of multicellular organisms very far apart in the filogenetic tree scales as the square root of the number of the genes, and that in critical networks the typical length of the cycles increases as a power law of system size, also consistently with the behavior of cell cycles time. Thus it is interesting to understand how these distributions look like in the limit of very large systems.

Another reason of interest of the present approach is that it allows to understand the limits of the annealed approximation. In our interpretation the annealed approximation is valid as far as the system loses memory of the details of its evolution. This, of course, does not happen if in a realization of a random network some structural properties that are able to influence its asymptotic dynamics emerge. Thus the approach presented here is complementary to the one used in [9].

3 Definition of the relevant elements

Let us start recalling the definition of the stable elements [5]. These are elements that evolve to a constant state, independent of the initial configuration. Flyvbjerg defined them and computed their fraction $s = S/N$ using the annealed approximation, which becomes exact in the infinite size limit. We now recall briefly, for future convenience, the main steps of this calculation.

Let us suppose that an element is controlled by $K - i$ stable elements and i unstable ones. Then it will be stable if the control function does not depend on the unstable arguments when the stable arguments assume their fixed values. Otherwise it will be unstable. When all the i unstable elements are different (this can always be taken to be the case if K is finite and N grows), the probability P_i to choose a constant control function of i binary variables is given by $P_i = p^{n_i} + (1 - p)^{n_i}$, with $n_i = 2^i$. In the framework of the annealed approximation, extracting at random connections and response functions at each time step, we get the following equation for the fraction of variables that are stable at time t :

$$s(t + 1) = \gamma(s(t)) = \sum_{i=0}^K \binom{K}{i} s(t)^{K-i} (1 - s(t))^i P_i. \quad (2)$$

This equation can be shown to be exact in the infinite size limit. The fixed point of this map (which can be interpreted as a self-consistency equation for the fraction of stable variables) has only the trivial solution $s = 1$ in the frozen phase, in other words all the elements are stable except eventually a number increasing less than linearly with N . In the

chaotic phase this solution becomes unstable and another solution less than 1 appears. This happens when $K(1 - P_1) = 1$. Since $1 - P_1 = \rho$ (it is just the probability that the response to two different signals are different) this condition is equivalent to the condition obtained from the study of the Hamming distance.

The existence of the stable variables is due to the finite connectivity of the network (s^* goes to zero very fast when K increases). These variables do not take part in the asymptotic dynamics. Among the remaining unstable variables, some are irrelevant for the dynamics, either because they do not send signals to any other variable, or because they send signals, but the response functions are independent of this signal when the stable variables have attained their fixed values. The remaining variables, that are unstable and control some unstable variable, are what we call the relevant variables. They are the only ones that can influence the long time behavior of the system.

To be more clear we now describe the algorithm that we used to identify the relevant variables. As a first step, we have to identify the stable variables. These are the variables that assume the same constant state in every limit cycle, and identifying them is computationally very hard, but very simple in principle. We then eliminate from the system the stable variables, reducing the response functions to functions of the unstable variables alone. Some of the connections left are still irrelevant, and we have to eliminate them (a connection between the elements i and j is irrelevant if the reduced response function $f_i(\sigma_{j_1(i)}, \dots, \sigma_{j_{K_i}(i)})$ does not depend on the argument σ_j for all the configurations of the remaining $K_i - 1$ control variables). At this point we iterate a procedure to eliminate the irrelevant variables. At each iteration we eliminate the variables that do not send any signal to anyone of the variables that are left, until we remain with a set that cannot be further reduced. This is the set of the relevant variables.

Measuring the number of relevant variables is computationally a very hard task. In order to identify the stable variables, in fact, we should find all the cycles in the network, and, to be rigorous, we should simulate a number of trajectories of the same order of the number of configurations in the system. Of course this is not feasible and we run only 200 (in some case 300) randomly chosen trajectories in every network. Thus we overestimate the number of stable elements. Nevertheless, the number of stable elements changes very little when we simulate more initial conditions and we think that the error that we make is not very large. However, for every network we simulate some hundreds of trajectories and every trajectories has to be followed until the closing time. This grows exponentially with system size in the chaotic phase. On the critical line the typical closing time increase roughly as a power law of system size, but the distribution becomes broader and broader and the average closing time is more and more dominated by rare events. The average depends thus on the number of samples generated and on the cutoff of the closing time, *i.e.* the maximum time that we are disposed to wait to look for a cycle. To reduce the bias determined by the cutoff, we had to run simulations lasting a time which increases roughly as a stretched exponential of system size on the critical line. Thus it is not possible to simulate systems of more than about one hundred elements in the chaotic phase and one thousands of elements on the critical line.

4 Scaling argument in the frozen phase

The mean field analysis [5] shows that the fraction of relevant variables vanishes in the frozen phase and on the critical line, but does not tell how the number of relevant variables scales with N as N grows. In order to clarify this point, we have to go beyond the mean field picture.

In the special case of $K = 1$, belonging to the frozen phase for every $\rho < 1$, there are detailed analytical results about the distribution of the relevant variables [6]. We propose here a rough argument that generalizes those results to the whole frozen phase and predicts that the typical number of relevant elements scales as \sqrt{N} on the critical line. Though this argument is based on some approximations which we can not control, its results coincide for $K = 1$ with the exact results by Flyvbjerg and Kjaer.

Let us suppose that we add a new element to a system with N elements, R of which are relevant, while S are stable and $I = N - R - S$ are indifferent, *i.e.* neither stable nor relevant. The probability that the new element is relevant can be computed as a function of R and S , within some approximations that we are going to discuss in a while. This probability is equal to the fraction of relevant elements in the system with $N + 1$ elements, given that the relevant elements are R and the stable ones are S in the system with N elements. We can then average over R and S in order to get an equation connecting $r_{N+1} = \langle R \rangle_{N+1} / (N + 1)$ to the moments of the distribution of R in the system with N elements. Since in the frozen phase and on the critical line r_N vanishes, it will be enough to consider the first two moments of the distribution, and the resulting equation can be solved asymptotically in N .

The weakness of this approach lies on the assumptions that allow us to express the probability that the new element is relevant as a function of R and S , as it will become soon clear. We compute now this probability. To this aim, we need two steps:

1. As a first step, we have to extract the K control elements and the response function of the new element. As a consequence, the new element can be stable, unstable or, if it receives an input from itself and this input is relevant in the sense discussed above, relevant. The evaluation of the stability is perfectly equivalent to the mean field argument, but this stability is only temporary because it can be altered by the second step described below. Thus we call a new element that is stable (unstable) after the first step a *temporarily* stable (unstable) element.
2. Then we have to send to the old system the signal of the new element. For each of the KN old control connections we have a probability $1/(N + 1)$ that the connection is broken and the old control element is substituted by the new element. This step perturbs the elements that control the new element and modifies its temporary stability. We have no chance to take this into account, unless we use some drastic approximations.

In the second step, three situations can occur.

1. If the new element was relevant in the first step, the new step can not modify this condition.
2. If the new element was unstable, it cannot become stable through the feedback of its signal. So it will be relevant or indifferent, depending on whether it sends an input to at least one relevant element or not.

3. If the new element was stable, its signal can destabilize some of the elements that control it and thus it can become relevant through a feedback mechanism, very hard to investigate analytically.

To compute the probability of case 3, we should know the organization of the network in the very detail and not only the number of relevant and stable elements. We propose to bypass this difficulty considering a different event: we will consider the new element relevant if it receives a signal from a previously relevant element or from itself. This is the simplest way to get a closed equation for the average number of relevant elements. In this way we make two errors of opposite sign: on one hand we overestimate the probability that a temporarily unstable element becomes relevant, on the other one we underestimate the probability that the new element is temporarily unstable and we neglect the probability that a temporarily stable element becomes relevant through a feedback loop.

We think that this method captures at least the qualitative behavior of the number of relevant elements. We have then to compare the estimate given by this approximation to the simulations, because the approximation is not under control. We present this argument because its results agree with both the numerical results and with the analytical calculations for $K = 1$ and because we believe that it is possible to improve this method and to keep the approximation under control.

Since we are interested in the frozen phase, where the fraction of unstable elements vanishes in the infinite size limit, we can neglect the eventuality that the new element is controlled by more than two elements that were relevant in the old system. The results are consistent with this assumption. With these approximations we obtain the following equation for the probability that the new element is relevant:

$$\begin{aligned} \langle r \rangle_{N+1} = \sum_{n=0}^N \Pr \{R_N = n\} & \left[K\rho \left(\frac{n+1}{N+1} \right) \left(1 - \frac{n+1}{N+1} \right)^{K-1} \right. \\ & \left. + \rho_2 \binom{K}{2} \left(\frac{n+1}{N+1} \right)^2 \left(1 - \frac{n+1}{N+1} \right)^{K-2} \right], \end{aligned} \quad (3)$$

where ρ_2 represents the probability that a Boolean function of two arguments is not constant and in terms of ρ is given by

$$\rho_2 = 1 - p^4 - (1-p)^4 = \rho \left(2 - \frac{\rho}{2} \right). \quad (4)$$

In the frozen phase it is sufficient to consider that the new element receives only one signal from the previously relevant elements. So, posing $c = K\rho$, the equation for the new fraction of relevant elements, r , is

$$\langle r \rangle_{N+1} \approx c \langle r \rangle_N + \frac{c}{N}. \quad (5)$$

The first term represents a new element that receives a relevant signal from one of the previously relevant elements, the second term represents a new element that receives its own relevant signal.

Thus the average number of relevant elements is independent on N and its asymptotic value is

$$\langle R \rangle_N = \frac{c}{1-c}. \quad (6)$$

This number diverges on the critical line $c = 1$. In this case, we have to consider also the eventuality that the new element receives a signal from two of the previously relevant elements. Expanding to the second order in $r = R/N$, and using the fact that $\rho_c = 1/K$, we get the equation

$$\langle r \rangle_{N+1} \approx \langle r \rangle_N - \left(\frac{K-1}{4K} \right) \langle r^2 \rangle_N + \frac{1}{N}, \quad (7)$$

whence, in the asymptotic regime where the variations of $\langle r \rangle_N$ are of order r/N , we finally get

$$\langle r^2 \rangle_N \approx \left(\frac{K-1}{4K} \right) \frac{1}{N}. \quad (8)$$

This means that the scale of the number of relevant elements grows, on the chaotic phase, as \sqrt{N} .

We stress here that these computations are valid because of the finite connectivity of the system. If we perform the limit $K \rightarrow \infty$ on the above result, we get that the scale of the number of relevant elements grow as $1/2\sqrt{N}$. If, instead, we apply the limit $K \rightarrow \infty$ prior to the limit $N \rightarrow \infty$ we get the trivial critical point $\rho = 0$, where all the elements are stable after one time step, while for every other ρ value all the elements are relevant. Thus, the two limits do not commute. In fact, the equation (2) for the fraction of stable variables and all the computations performed in this section are valid only if we can neglect that the same element is chosen more than once to control a given element, *i.e.* for $K \ll N$.

The result (6) coincides for $K = 1$ with the analytical computation by Flyvbjerg and Kjaer [6], thus suggesting that the distribution of relevant elements is independent on N in the whole frozen phase, and depends on the two parameters K and ρ only through their product. This picture agrees with the results of the annealed approximation, which predicts that the distribution of the number of different elements in two asymptotic configurations is independent on N and depends only on the product of the parameters K and ρ in the frozen phase [9].

Our simulations confirm that on the critical line the number of relevant elements scales as \sqrt{N} (see figure 6). Also the annealed approximation is consistent with this result, since it predicts that the number of elements whose state is different in two asymptotic configurations has to be rescaled with \sqrt{N} on the critical line [9]. On the other hand the number of unstable elements grows much faster with N (numerically it is found that it goes as $N^{3/4}$, see below) but this discrepancy is only apparent, since the asymptotic Hamming distance is related more to the number of relevant elements than to this quantity.

For later convenience (see our next paper) it is also interesting to compute the effective connectivity, defined as the average value of the relevant connections between relevant elements. Let us compute it by imposing the condition that the network has R relevant elements.

The effective connectivity is equal to the average number of connections between the new element and the other relevant elements of the older system, with the condition that the new element is relevant. From equation (3) we have, at the leading order in R/N :

$$K_{eff}(R) = \frac{c \frac{R}{N} \left(1 - \frac{R}{N}\right)^{K-1} + 2\rho_2 \binom{K}{2} \left(\frac{R}{N}\right)^2 \left(1 - \frac{R}{N}\right)^{K-2}}{c \frac{R}{N} \left(1 - \frac{R}{N}\right)^{K-1} + \rho_2 \binom{K}{2} \left(\frac{R}{N}\right)^2 \left(1 - \frac{R}{N}\right)^{K-2}} \quad (9)$$

$$\approx 1 + A(K, \rho) \frac{R}{N}.$$

This equation shows that the effective connectivity minus 1 goes to zero as R/N in the frozen phase (where $R/N \propto 1/N$) and on the critical line (where $R/N \propto 1/\sqrt{N}$). For a fixed system size, the effective connectivity increases linearly with the number of relevant elements.

5 Numerical results

5.1 Magnetization and stable elements

As a first step, our algorithm has to identify the stable elements. It does this by measuring their magnetization. We thus discuss our numerical results starting from this quantity.

The magnetization m_i^α of element i on the cycle Γ_α can be defined as the average activity of the element along the cycle:

$$m_i^\alpha = \frac{1}{L_\alpha} \sum_{C \in \Gamma_\alpha} \sigma_i(C). \quad (10)$$

The distribution of this variable, shown in figure 1 for $K = 3$ and $N = 75$, has many peaks, corresponding to simple rational values. This perhaps reflects the fact that the relevant elements are divided into asymptotically independent modules, so that a cycle can be decomposed into several independent shorter cycles. This subject will be further discussed in our second paper.

Our results have to be compared to the analytical work by Derrida and Flyvbjerg [13]. They defined the magnetization of element i at time t on a given network as the activity of the element at time t averaged over many initial configurations and could compute analytically its stationary distribution, in the limit $N \rightarrow \infty$, using the annealed approximation, that can be shown to be exact for this purpose. The picture they got is different from ours, in particular we see peaks much higher than theirs. For instance the peak at $|2m - 1| = 1$, which gives information on the size of the stable core of the network, is about 10 times larger than expected, and the first moments of the magnetization, that can be computed analytically, are larger than the predicted values. Thus we performed other simulations that strongly suggest that these discrepancies are finite size effects, and we present an argument that explains their origin.

In order to investigate larger systems we had to change the definition of the magnetization. The definition (10) is numerically cumbersome, since the measure takes place only after that a cycle has been found, and this means, for chaotic systems, that we have to wait a time exponentially increasing with N . Thus we neglected this condition and we measured the magnetization of the variable i at time t as the average activity of the variable with

respect to different initial conditions (this definition coincides with the one used by Derrida and Flyvbjerg). For very large t , when all trajectories have reached a limit cycle, this quantity tends to the asymptotic value

$$m_i = \sum_{\alpha} W_{\alpha} m_i^{\alpha}, \quad (11)$$

where W_{α} is the weight of the basin of cycle Γ_{α} and m_i^{α} is defined in (10). We observed that $m(t)$ reaches a stationary value (within some precision) much earlier than the typical time at which the trajectories reach their limit cycles. At first sight surprisingly, the time after which $m(t)$ reaches its stationary distribution does decrease with system size instead of increasing (see figure 2).

We measured the second and fourth moment of the magnetization in a system with $K = 3$ and $\rho = 1/2$, and we found a large positive correction to the infinite size values computed by Derrida and Flyvbjerg [13]. The values found coincide within the statistical error with those obtained from equation (10) for a system of small size for which we did an explicit comparison. These values can be fitted to the sum of the infinite size value, that we got from [13], plus an exponentially decreasing term. The exponent of the best fit turned out to be the same for both the moments that we measured: we found $m_2(N) \approx 0.236 + 0.24 \cdot \exp(-N/70)$, and $m_4(N) \approx 0.128 + 0.26 \cdot \exp(-N/70)$.

The measure of the magnetization allows to identify the stable elements as the elements with $\sum_{\alpha} W_{\alpha} m_i^{\alpha}$ equal either to 0 or to 1. The two definitions of the magnetization gave roughly the same number of stable elements in the cases where we could compare the results, but with the second method we could consider much larger systems (we recall that the difference between the two methods is that in the first case a cycle has been reached while in the second one the system is still in some transient configuration). The second method was used only to study finite size effects, since it does not allow to identify the relevant elements (see below).

Both the methods overestimate the number of stable elements, since it could happen that an element appearing stable in our sample of trajectories (some hundreds) oscillates in a cycle that is not reached by any of them. We checked that the results do not change qualitatively if we consider a larger number of trajectories.

The fraction of stable nodes measured in simulations with $K = 3$ and N ranging from 50 to 200 have been compared to the prediction of the mean field theory by Flyvbjerg. The networks with $N = 50$ have a stable core about 10 times larger than the mean field value (in this case we measured the magnetization using both the above definitions, while for larger systems only equation (11) was used). The corrections to the mean field value, that is exact in the infinite size limit, appear to decay exponentially with a rate identical, within statistical errors, to the decay rate of the corrections to the moments of the magnetization: we found $s(N) \approx 0.0122 + 0.21 \cdot \exp(-N/70)$.

For every size of the systems which we simulated the stable core is then much larger than it would be in an infinite system. On this ground, we may expect very important finite size effects concerning the dynamical properties of the system.

Summarizing, the distribution of the magnetization for finite systems has the following

characteristic: 1) The asymptotic value is reached after a time that *decreases* with system size; 2) the corrections to the infinite size values are very large; and 3) these corrections decrease exponentially with system size. These apparently strange finite size effects have a simple interpretation: they arise as a consequence of the periodic dynamic of the random networks.

The mean field values of the magnetization and of the stable core are computed within the annealed approximation without taking into account the fact that the asymptotic dynamic is periodic. As we proposed in [9], the existence of limit cycles must be taken into account in the framework of the annealed approximation in this way: if at time t all the configurations generated are different (*i.e.* the trajectory is still open) we treat the quantities of interest (distance, magnetization or stable core) as a Markovian stochastic process; if one configuration has been found twice (the trajectory is closed) we impose the condition that all quantities are periodic. Thus the master equation for the distribution for the number of stable variables is, in the framework of the annealed approximation:

$$\begin{aligned} \Pr \{S(t+1) = S', O(t+1) \mid S(t) = S, O(t)\} &= \binom{N}{S'} (\gamma(s))^{S'} (1 - \gamma(s))^{N-S'} (1 - \pi_N(S, t)) \\ \Pr \{S(t+1) = S', \overline{O(t+1)} \mid S(t) = S, O(t)\} &= \binom{N}{S'} (\gamma(s))^{S'} (1 - \gamma(s))^{N-S'} \pi_N(S, t) \\ \Pr \{S(t+1) = S', \overline{O(t+1)} \mid S(t) = S, \overline{O(t)}\} &= \delta_{SS'}, \end{aligned} \quad (12)$$

where $S(t)$ is the number of stable elements, $s = S/N$, $O(t)$ stands for the condition that the trajectory is open at time t (no configuration has been visited twice), $\overline{O(t)}$ stands for the condition complementary to $O(t)$ (the trajectory has closed on a previously visited configuration) and $\pi_N(S, t)$ is the probability that a trajectory open at time t and with S stable elements at time $t+1$ closes at that time. Finally, $\gamma(s)$ is given by equation (2).

We don't know how to compute $\pi_N(S, t)$, but it is clear that this is an increasing function of S for fixed t : the more elements are stable, the more it is likely that the trajectory closes. The infinite size value of the stable core is given by equation (2), that represents the evolution of the most probable number of stable variables. It is clear that the corrections to this value are positive, and that they go to zero as soon as the closing time becomes much larger than the time necessary for the stable core to reach its stationary value in an infinite system (where all trajectories are still open). Thus we expect that these corrections vanish as a power law of the typical length of the cycles: in the chaotic phase this means that the finite size corrections due to this effect vanish exponentially with system size, as we observed simulating systems with $K = 3$ and $\rho = 1/2$. Lastly, this argument implies that the time after which the distribution of the stable elements becomes stationary is shorter in an infinite system than in a small system, where the evolution of $S(t)$ is coupled to the closure of the periodic orbits. Thus the correction of the annealed approximation to take into account the existence of periodic attractors can account for all the features of the finite size effects that we observed.

5.2 The relevant elements in the chaotic phase

After having identified the stable elements we detect the relevant elements using the algorithm described in the second section and we study how this quantity influences the dynamical properties of the network. The main results are that the average cycle length grows almost exponentially with the number of relevant variables in some range of this variable and the average weight of the attraction basins has apparently a non monotonic behavior versus the number of relevant variables. This qualitative features are the same both in the chaotic phase and on the critical line, but the ranges of R in which these things happen are quite different in the two cases. We start discussing the situation in the chaotic phase.

The simulations were done generating at random 20,000 sample networks and running 200 trajectories on each of them. The parameters considered in this section are $K = 3$, $\rho = 1/2$ and system size N ranging from 30 to 60 elements.

Figure 3 shows the density of the distribution of the fraction r_N of relevant variables, $r_N = R/N$. The density relative to the most probable value increases with system size, and it appears that r_N tends to be delta-distributed in the infinite size limit, as it is expected on the ground of the annealed master equation (12). We observe an excess of networks with very few relevant elements (*i.e.* very many stable elements), consistently with the finite size effects discussed in last section. This excess seems to disappear in the infinite size limit.

Then we show the average length of the cycles in networks with R relevant elements (figure 4). This quantity increases almost exponentially with R when $r = R/N$ is large, while its behavior is different for small r . The crossover takes place at about $r = 0.5$. Thus the number of relevant elements turns out to have a very important influence on the typical length of the cycles

We have also measured the conditional distribution of the length of the cycles in networks with R relevant elements. When R is close to N the distribution decays as a stretched exponential with an exponent smaller than one, very close to the one found in the unconditioned distribution. Thus the deviation of the unconditioned distribution from the prediction of the annealed approximation, that predicts a much narrower distribution, is not a consequence of the existence of the relevant elements.

The other quantity that we measured is the average weight of the attraction basins, Y_2 , defined by the equation

$$Y_2 = \sum_{\alpha} W_{\alpha}^2, \quad (13)$$

where W_{α} is the attraction basin of cycle α . We used the method proposed by Derrida and Flyvbjerg [4], that is based on the fact that Y_2 is equal to the probability that two trajectories chosen at random end up on the same attractor.

From our data (not shown) it appears that Y_2 has a non monotonic behavior as a function of r : for very small r it decreases from the value 1, corresponding to $r = 0$, reaches a minimum and rapidly increases. At large r , Y_2 does not seem to be correlated with r (at least within the statistical error, that is rather large). We will see in the next paper that the decreasing behavior at small r can be interpreted as an effect of the modular organization of Kauffman networks.

5.3 Relevant elements on the critical line

We simulated systems with $K = 4$ and the critical value $\rho = 1/4$. Systems size ranges from 120 to 1600. Concerning the statistical properties of the attractors, these networks have a behavior very similar to that of the more studied $K = 2$, $\rho = 1/2$ networks [10].

In these networks, the number of relevant elements appears to scale as \sqrt{N} , in agreement with the argument presented in section 4. The number of unstable elements, on the other hand, appears to scale as $N^{3/4}$. This implies that the probability to extract at random an element which is relevant, scaling as $N^{-1/2}$, is approximately proportional to the square of the probability to extract at random an element which is relevant ($N^{-1/4}$).

These scaling laws can be observed both looking at the average quantities and looking at the whole distribution. The average number of unstable variables is found to follow the power law $U \propto N^a$, with $a = 0.74 \pm 0.01$. We then define the rescaled variable $x_u = U/N^{3/4}$, and we compare its probability density for various system sizes. As it can be seen in figure 5 the different curves superimpose within the statistical errors. This suggests that x_u has a well defined probability density in the infinite size limit, although our data are rather noisy to state this point without doubts. We can distinguish in the distribution three different ranges with different characteristics: at vanishingly small values of x_u (ranging from $U = 0$ up to $U = 4$) the density decreases very fast. At intermediate values, roughly up to $x_u = 1$, it looks to decrease approximately as a power law with a small exponent (the best fit exponents that we found range from 0.25 to 0.40, showing some tendency to increase with system size). Asymptotically, for large x_u , the best fit is a stretched exponential, $f(x) \approx \exp(-Cx^\beta)$, with an exponent compatible with $\beta = 1.7 \pm 1$ for all the systems that with studied with N larger than 240.

The number of relevant variables was studied in a similar way. Its average value increases as a power law of N , $\langle R \rangle \propto R^b$, with $b = 0.52 \pm 0.02$. The rescaled variable $x_r = R/\sqrt{N}$ looks to have a well defined distribution in the infinite size limit, as it is shown in figure 6, where the probability density of x_r is plotted for system sizes ranging from 120 to 1600. For large x the density of the distribution is well fitted by a stretched exponential, $\exp(-Cx^\beta)$, with the exponent β compatible with the value $\beta = 0.56 \pm 0.02$ for system size larger than 240.

The average length of the cycles increases exponentially as a function of the number of relevant elements, for r large, and more slowly for r small, just as it happens in the chaotic phase. Figure 7 shows on a logarithmic scale the behavior of the average length of the cycles as a function of the rescaled number of relevant elements, $x_r = R/\sqrt{N}$, for different system sizes at the critical point $K = 4$, $\rho = 1/4$.

The average weight of the attraction basins, Y_2 , has a non monotonic behavior as a function of the number of relevant elements, as it happens in the chaotic phase. The value of $Y_2(R)$ is one for $R = 0$, then decreases to a minimum value and increases very slowly, as it is shown in figure 8, where $\overline{Y_2}$ is plotted against $x_r = R/\sqrt{N}$, for $K = 4$, $\rho = 1/4$ and different system sizes.

Nevertheless, there are two important differences with respect to the chaotic phase: first, the range where $Y_2(R)$ is a decreasing function is much wider on the critical line than in the chaotic phase; then, on the critical line the curves corresponding to a smaller N value are

lower, while in the chaotic phase the contrary holds. As a consequence, if we average $Y_2(R)$ over R on the critical line, we get a quantity vanishing in the infinite size limit [10], while the average weight of the attraction basins is finite and very close to the Random Map value in the chaotic phase [9].

This difference and the non monotonic R behavior of $Y_2(R)$ have a clear interpretation in the framework of the modular organization of Kauffman networks [8]. We thus postpone to that paper the discussion of our results.

References

- [1] S.A. Kauffman (1969), Metabolic Stability and Epigenesis in Random Constructed Genetic Nets, *J. Theor. Biol.* **22**, 437-467. S.A. Kauffman (1993), *Origins of Order: Self-Organization and Selection in Evolution*, Oxford University Press
- [2] Derrida B. and Y. Pomeau (1986), Random Networks of Automata: a Simple Annealed Approximation, *Biophys. Lett.* **1(2)**, 45-49
- [3] B. Derrida and G. Weisbuch (1986), *J. Physique* **47** 1297. H.J. Hilorst and M. Nijmayer (1987), *J. Phys. Paris*, **48**, 185.
- [4] B. Derrida and H. Flyvbjerg (1986), Multivalley Structure in Kauffman's Model: Analogy with Spin Glasses, *J.Phys.A: Math.Gen.* **19**, L1003-L1008
- [5] H. Flyvbjerg (1988), An Order Parameter for Networks of Automata, *J.Phys. A:Math.Gen.* **21** L955-L960
- [6] H. Flyvbjerg, N.J. Kjaer (1988), Exact Solution of Kauffman Model with Connectivity One, *J.Phys. A:Math.Gen.* **21(7)**, 1695-1718
- [7] M. Mezard, G. Parisi, M.A. Virasoro (1987), *Spin Glass Theory and Beyond*, Singapore: World Scientific
- [8] U. Bastolla and G. Parisi (1997), The modular structure of Kauffman networks, *Physica D*
- [9] U. Bastolla and G. Parisi (1996), Closing Probabilities in the Kauffman model: an Annealed Computation, *Physica D* 98, 1.
- [10] U. Bastolla and G. Parisi (1996), The critical line of Kauffman networks, *Journal of Theoretical Biology*, in press.
- [11] B. Derrida, H. Flyvbjerg (1986), The random map model: a disordered model with deterministic dynamics, *Journal de Physique* **48**, 971-978
- [12] A. Bhattacharijya and S. Liang (1996), Power-Law Distribution in the Kauffman Net, *Physica D*
- [13] B. Derrida and H. Flyvbjerg (1987), Distribution of Local Magnetizations in Random Networks of Automata, *J.Phys.A: Math.Gen.* **20**, L1107-L1112.

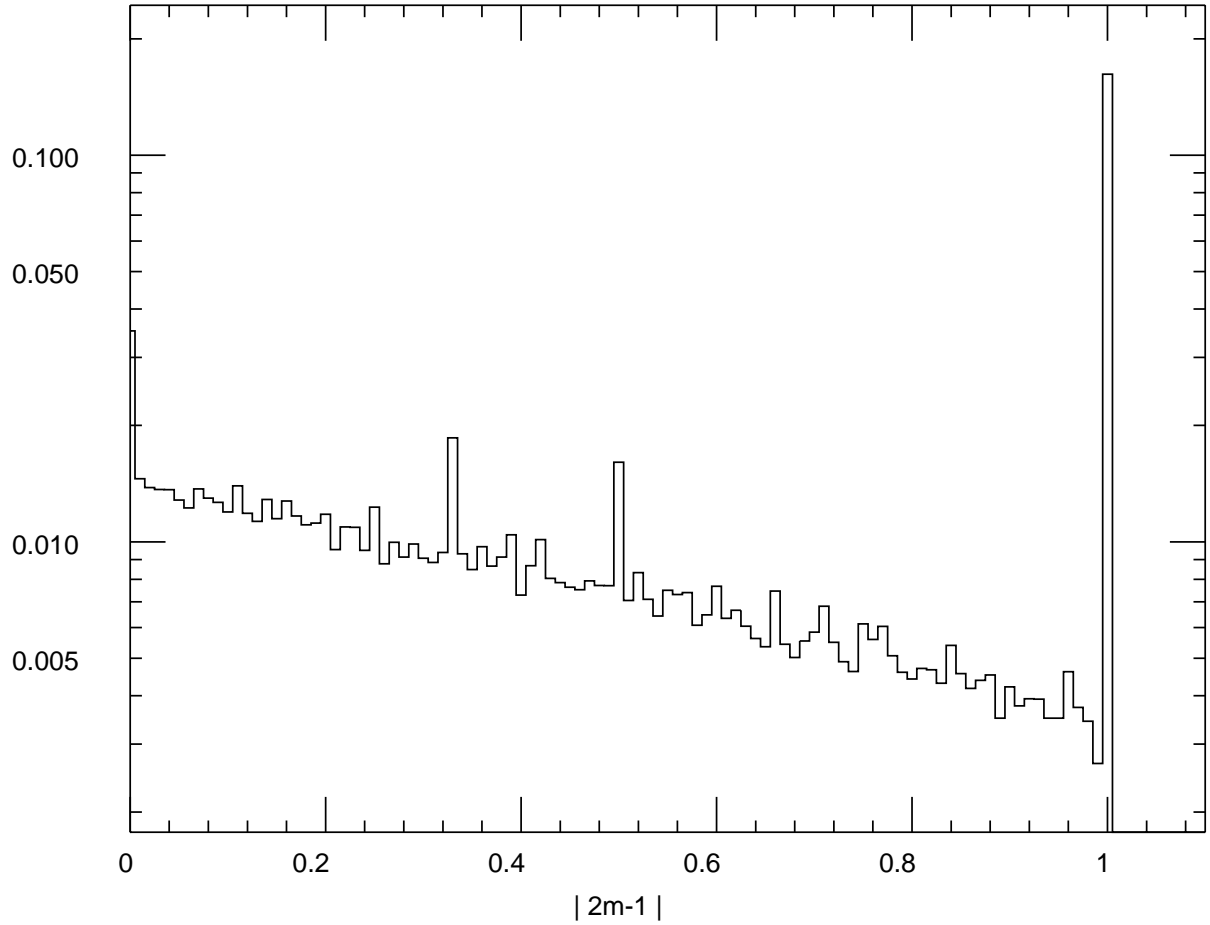


Figure 1: *The histogram of $|2m - 1|$, where m is the average activity of a given node in a single cycle of a given network, is shown for $K = 3$ and $N = 75$. The peaks correspond to simple rational values of the argument: for instance, $1/8, 1/7, 1/6 \dots$ 800 sample networks were generated, and 500 trajectories simulated on each of them.*

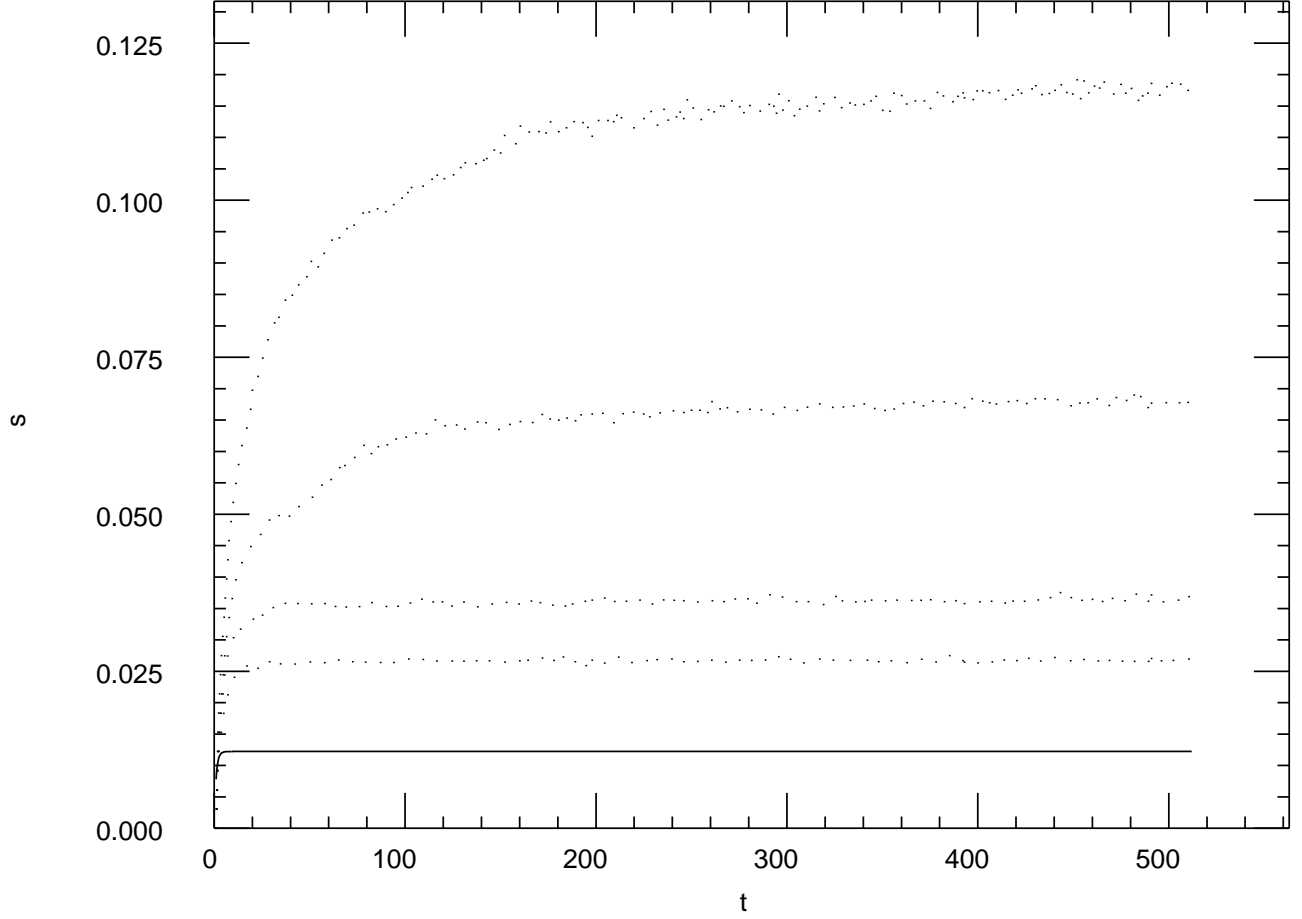


Figure 2: *Fraction s of nodes which are at time t in the same state in all the 200 different trajectories simulated. Data are average over 200 sample networks. $K = 3$, $N = 50, 100, 150$ and 200 (N grows from top to bottom). The solid line is the mean field equation, $s(t+1) = \sum_{l=0}^K \binom{K}{l} s(t)^{K-l} (1-s(t))^l \frac{1}{2^{2^l-1}}$.*

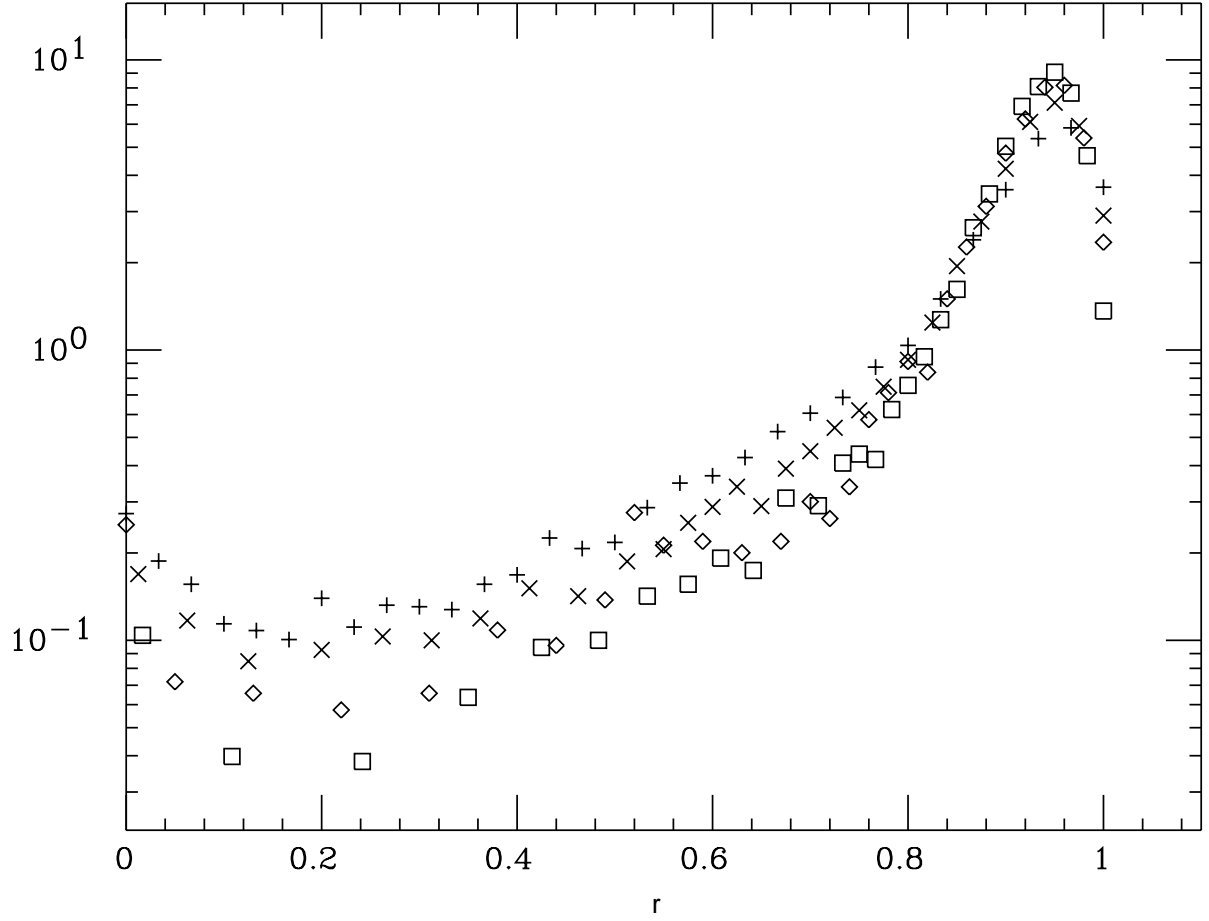


Figure 3: *Histogram of the networks with a fraction r of relevant elements. $K = 3$, $N = 30$ (+), 40 (X), 50 (\diamond) and 60 (*). The networks generated were 20000, the relevant elements were identified simulating 200 trajectories on each of them.*

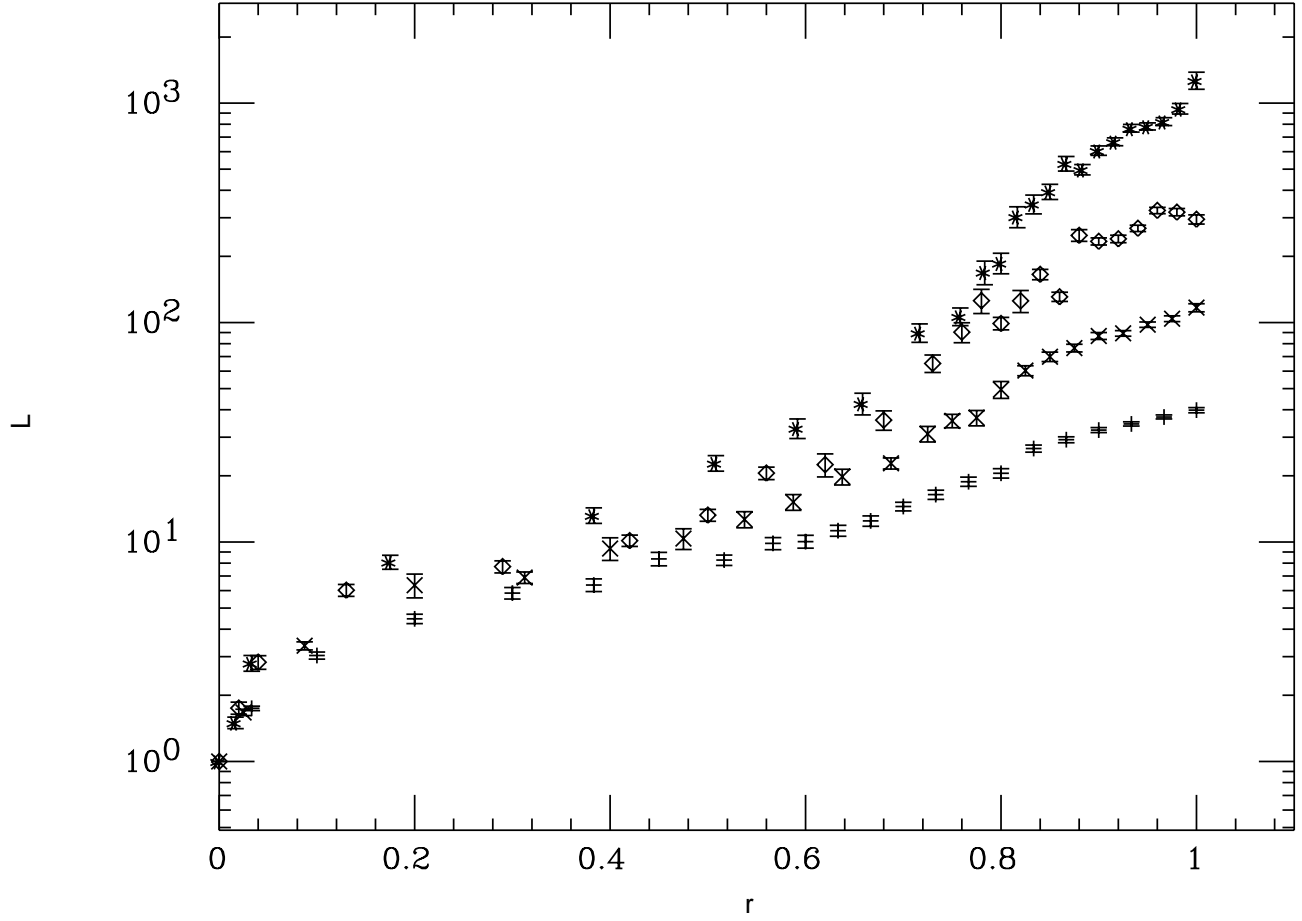


Figure 4: *The average period in networks with a fraction r of relevant nodes. $K = 3$, $N = 30, 40, 50$ and 60 . Each curve was obtained generating at random 20000 networks and simulating 200 trajectories on each of them.*

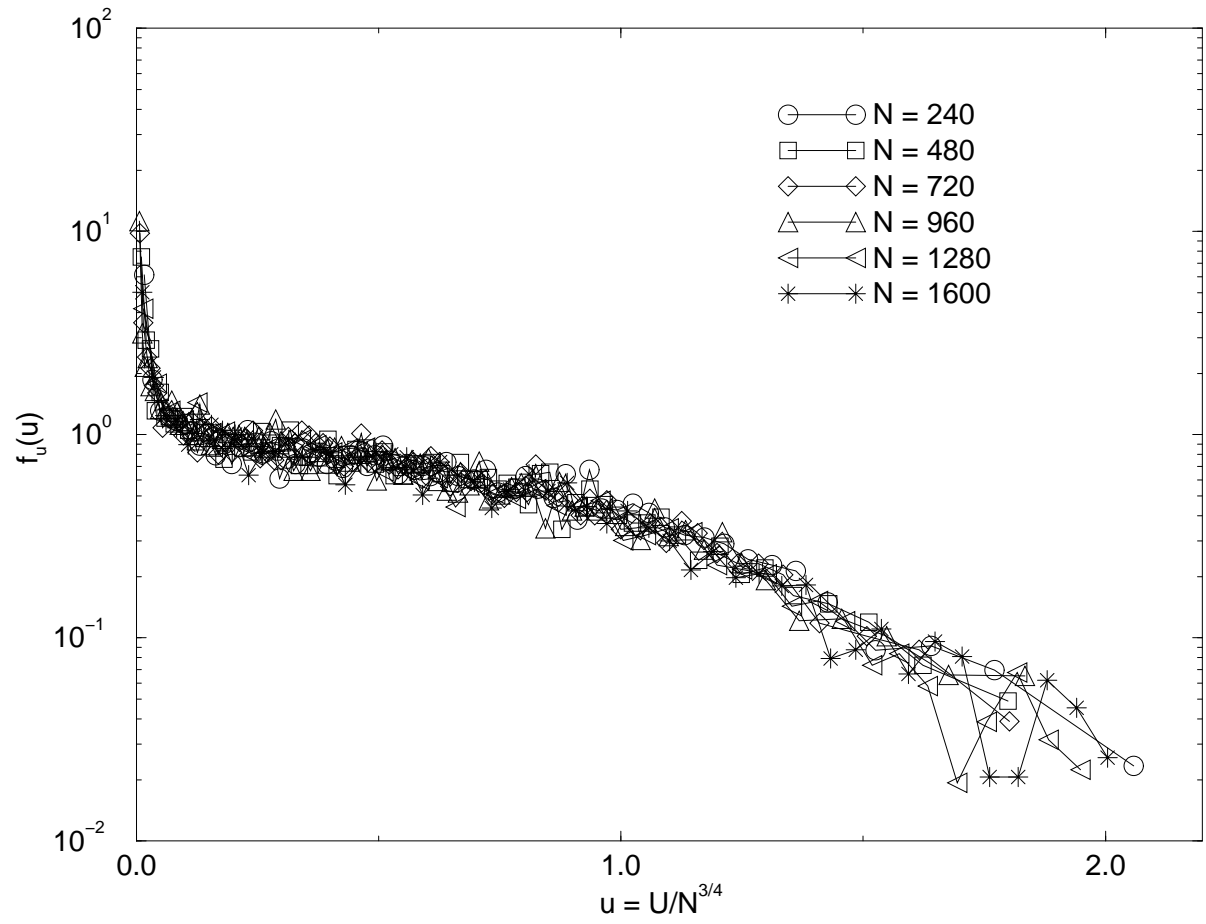


Figure 5: *Probability density of the rescaled number of unstable elements $x_u = U/N^{3/4}$, where U is the number of unstable elements in a random network. The systems are at the critical point $K = 4$, $\rho = 1/4$ and system size ranges from 240 to 1600.*

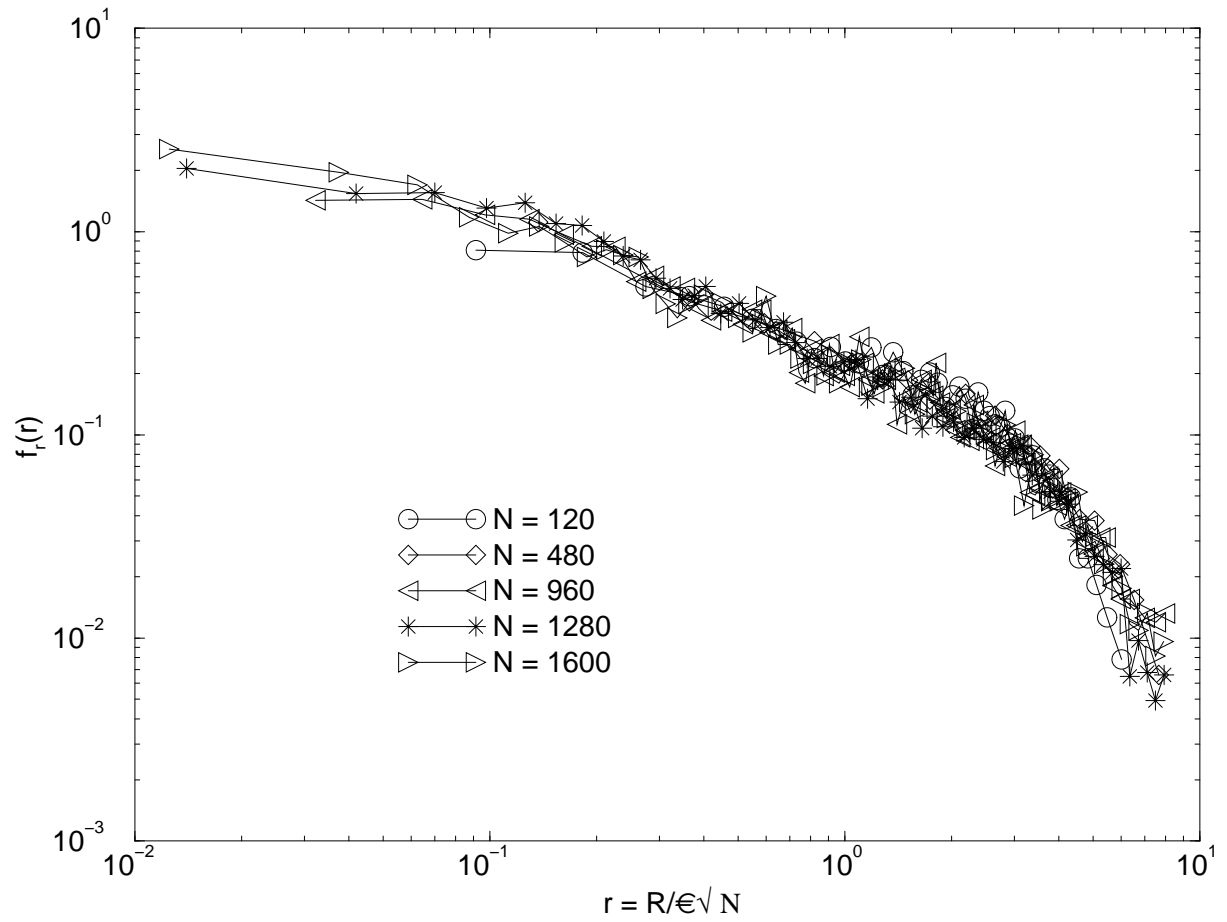


Figure 6: *Probability density of the rescaled number of relevant elements $x_r = R/N^{1/2}$, where R is the number of relevant elements in a random network. The systems are at the critical point $K = 4$, $\rho = 1/4$ and system size ranges from 120 to 1600.*

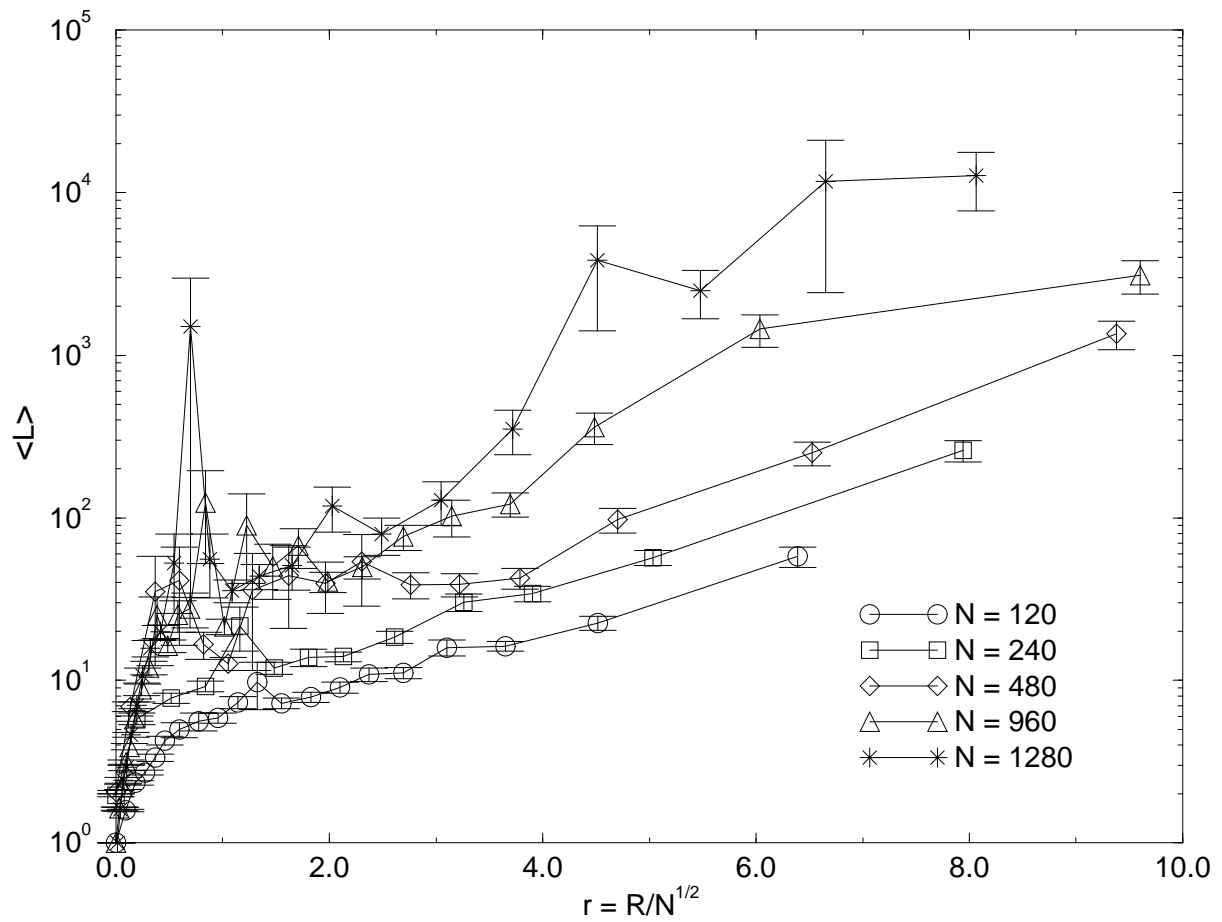


Figure 7: Average cycle length in networks with R relevant elements as a function of the rescaled variable $r = R/N^{1/2}$, for critical systems ($K = 4$, $\rho = 1/4$) of size ranging from 120 to 1600.

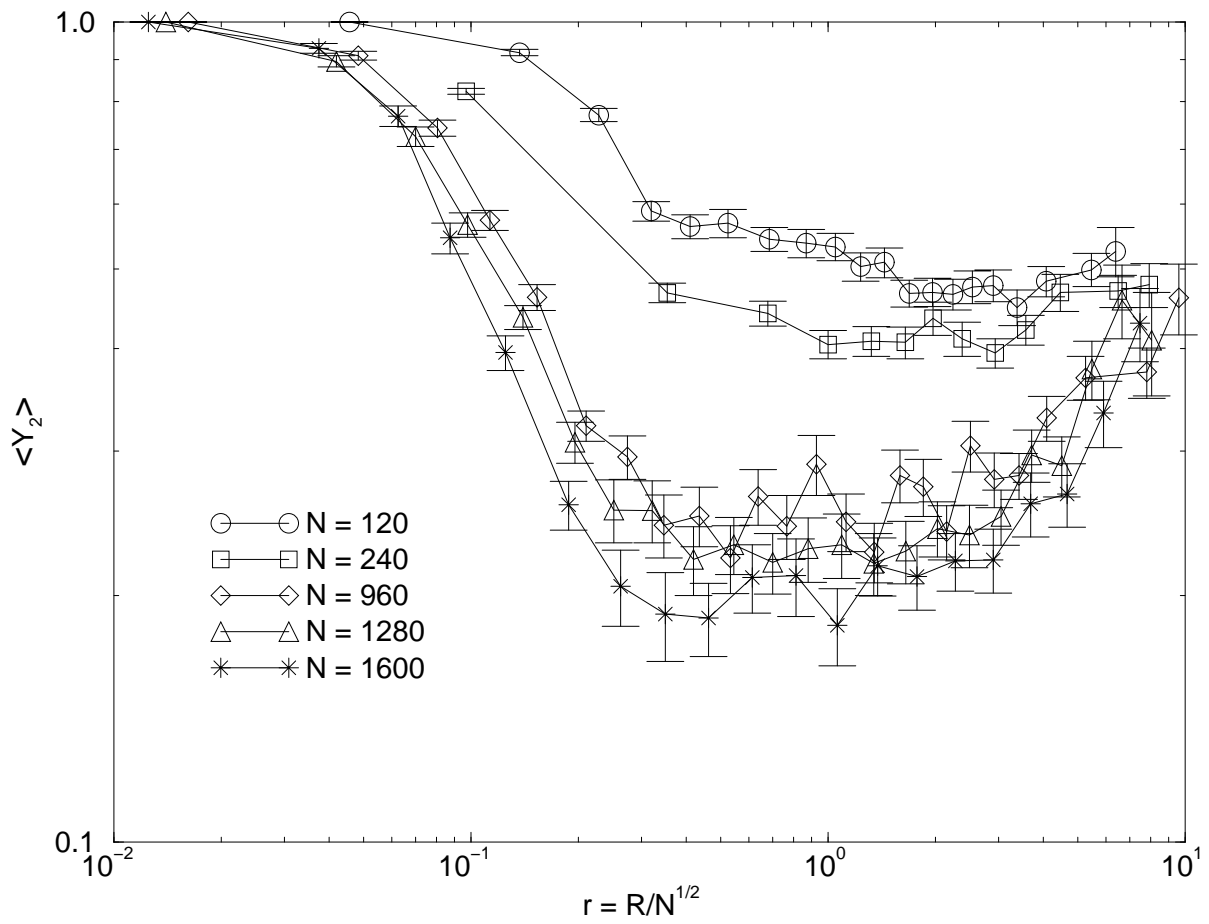


Figure 8: Average value of Y_2 in networks with R relevant elements, as a function of the rescaled variable $r = R\sqrt{N}$, for critical systems ($K = 4$, $\rho = 1/4$) of size from 120 to 1600.